

Seasonal priority effects: implications for invasion and restoration in a semi-arid system

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Summary

1. The timing of seasonal activity (i.e. phenology) may play an important role in plant invasions. In ecosystems characterized by seasonal rainfall, early-active exotic species may pre-empt resources and attain competitive dominance via a seasonal 'priority advantage'. Exotic annual grasses in California are often active earlier than native species, potentially because they possess greater germination plasticity. While these problematic invaders may usually benefit from having early phenology, their flexible germination cues might be manipulated as a restoration strategy to germinate seeds far in advance of favourable growing conditions, leading to a 'priority disadvantage'.

2. We manipulated the start of the growing season in an invaded California coastal sage scrub community characterized by a Mediterranean-type climate to (i) identify whether early-season phenology confers a performance advantage and (ii) test whether rainfall timing could be manipulated to favour native species. We compared the performance of seeded native and exotic focal species under ambient rainfall timing (winter rains) vs. with a pre-growing season (late-summer) watering event.

3. Under ambient rainfall timing, exotic annual grasses and forbs germinated earlier and reached higher levels of abundance than native species, consistent with a seasonal priority advantage. Many exotic annual grasses germinated with pre-season watering, but none survived until the onset of natural rains. Observations suggest that early-germinating seedlings suffered mortality via herbivory. The watering pulse thus depleted the exotic seedbank, fewer exotic individuals germinated with winter rains, and exotic species attained lower abundance than under the natural rainfall timing.

4. Native species, whether annual or perennial, did not germinate with the pre-season watering pulse, suggesting they may have more constrained germination cues than the exotic species.

5. *Synthesis and applications.* Our results suggest that phenology is an important factor influencing invasion success, and that this could be manipulated to favour native species. Manipulation of the start of the growing season, for example through a pre-growing season watering event, could be a successful restoration strategy for native species in some ecosystems.

Key-words: community assembly, community ecology, ecological restoration, exotic annual grass, germination, invasive species, phenology, rainfall, seasonality

Introduction

Invasive species have long fascinated ecologists as natural experiments in community assembly (Elton 1958; Sax *et al.* 2007), because they offer a window into the fundamental mechanisms that allow a new species to successfully invade an established community. From an applied perspective it is important to identify these mechanisms because large-scale exotic plant invasions threaten native biodiversity, alter ecosystem functioning, and have great economic costs (Mack *et al.*

2000; Pimentel, Zuniga & Morrison 2005). Disturbance (Hobbs & Huenneke 1992), resource pulses (Davis, Grime & Thompson 2000), high propagule pressure (Lonsdale 1999; Colautti, Grigorovich & MacIsaac 2006), release from natural enemies (Liu & Stiling 2006), or novel weapons (Callaway & Ridenour 2004) all may contribute to the establishment and subsequent success of invasive species. Additionally, exotic species may invade because they fill a 'vacant ecological niche', using different pools of resources than the native community (Elton 1958; Davis, Grime & Thompson 2000; Shea & Chesson 2002). Timing may also play a critical role in invasion, but has received considerably less attention than other contributing mechanisms. For instance, priority effects, or the impacts

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of early-arriving species on those arriving later in a system, can allow exotic species to colonize when they establish first and subsequently pre-empt resources on disturbed patches (Belyea & Lancaster 1999; Young, Chase & Huddleston 2001; Seabloom *et al.* 2003b). Priority effects could also operate seasonally on a within-year scale (Grman & Suding 2010), as exotic species may fill a ‘vacant phenological niche’ by being active earlier in the growing season than native species (Wolkovich & Cleland 2011). Early phenology may confer a competitive advantage via a seasonal priority effect (Fig. 1a), where the first individuals to become active pre-empt both space and associated resources (Young, Chase & Huddleston 2001).

In seasonal environments with a high abundance of annual plant species, germination plasticity could enable the establishment of exotic species via seasonal priority effects (Grime *et al.* 1981; Espigares & Peco 1993; Reynolds, Corbin & D’Antonio 2001). In general, plasticity can facilitate exotic invasion success through rapid growth responses (allowing exotics to capitalize on resource pulses), or by permitting growth under a wider breadth of environmental conditions than native species (Richards *et al.* 2006; Davidson, Jennions & Nicotra 2011). Small threshold watering events often trigger rapid annual grass germination in semi-arid systems (Went 1949; Tevis 1958) and may explain why exotic annual grasses germinate with small rain events and are typically active earlier in the growing season than many native species (Heady 1958; Pitt & Heady 1978; Hobbs & Mooney 1985; Deering & Young 2006). Although the concept of seasonal priority effects has not been tested previously, research has shown that annual grasses can

gain a competitive foothold via among-year priority effects in both Hawaii (D’Antonio, Hughes & Vitousek 2001) and California (Corbin & D’Antonio 2004; Lulow 2006). Further, numerous studies have shown that early-season activity and high growth rates of exotic annual grasses confer early access to resources (Booth, Caldwell & Stark 2003; Seabloom *et al.* 2003b; Hawkes *et al.* 2006; DeFalco, Fernandez & Nowak 2007; Abraham, Corbin & D’Antonio 2009). This resource pre-emption and fast growth rate can enable suppression of native seedlings (Eliason & Allen 1997; Carlsen, Menke & Pavlik 2000; Coleman & Levine 2007).

Understanding the extent to which priority effects contribute to community structure and assembly may aid in devising restoration strategies for invaded communities (Young, Chase & Huddleston 2001). Having flexible germination cues may facilitate invasions in some cases (Hierro *et al.* 2009), but could also incur a cost if seeds germinate before the growing season has truly begun (Bartolome 1979). While priority effects are generally considered advantageous (Fig. 1a), becoming active too early could result in ‘priority disadvantage’ (Fig. 1b). In semi-arid and Mediterranean-type ecosystems with a defined rainy season, a small pre-growing season rain event may prompt exotic germination. However, germinated individuals may then die due to desiccation without further rains, or they may succumb to herbivory because pre-season activity can increase apparency to herbivores (Lambrinos 2006). Thus, manipulation of early season germination may be an important restoration tool that could lower the abundance of exotic annual grasses (Marushia, Cadotte & Holt 2010), provided that barriers to survival result in a priority disadvantage.

Exotic annual grasses in California are an example of an invasion in a Mediterranean-type ecosystem that may be promoted by seasonal priority effects. Invasive European grass species introduced during the 18th and 19th centuries have impacted considerable portions of California’s renowned diversity of endemic vegetation (Crampton 1974; Baker 1989). By 1991, it was estimated that the range of annual grasslands in California had increased by at least three orders of magnitude relative to ranges at the beginning of the 19th century while virtually all other plant communities had undergone substantial declines (Barbour *et al.* 1991). Several factors have been proposed to explain the expansion of exotic annual grasslands in California, including periods of drought and altered fire and grazing regimes (D’Antonio *et al.* 2007; Minnich 2008). The distinctly early phenology of exotic annual grasses may also have promoted their invasion by allowing them to occupy an earlier phenological niche than resident plant species (Godoy *et al.* 2009; Wolkovich & Cleland 2011).

Here, we used a novel approach to explore the relationship between rainfall timing and the establishment of exotic annual grasses in southern California coastal sage scrub. Our objectives were twofold, to investigate: (i) whether seasonal priority effects are contributing to community-level patterns of abundance and (ii) whether pre-growing season watering could be a feasible technique to cause a priority disadvantage for invasive grasses and aid in California coastal sage scrub restoration efforts. We used field experimentation in the form

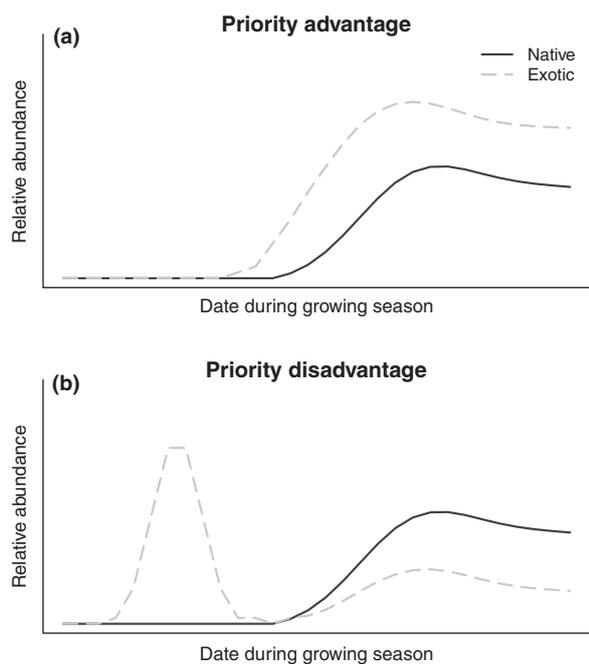


Fig. 1. (a) Exotic species could have a ‘priority advantage’ if they become active earlier in the growing season than native species, pre-empting resources and thus reaching higher abundances. (b) If exotic species become active before the onset of favorable environmental conditions that usually signal the start of the growing season, exotic species may be subject to a ‘priority disadvantage’ via physiological stress or apparency to herbivores.

of a pre-growing season (late summer) irrigation pulse applied to a disturbed and invaded coastal sage scrub community. We predicted that exotic annual grasses would benefit from a seasonal priority effect under ambient rainfall timing. We also predicted that exotic annual grasses would germinate in response to the early pulse of water, while native species would instead germinate later in response to cool temperatures combined with higher soil moisture, characteristic of the winter rainy season (Levine, McEachern & Cowan 2008). This early germination would confer a priority advantage only if individuals survived until the onset of the true growing season rains; reduced survival of early-germinating seedlings would provide evidence that flexible germination cues could be manipulated to confer a priority disadvantage in the context of restoration.

Materials and methods

EXPERIMENTAL SITE

We conducted our study at the University of California Scripps Coastal Reserve in San Diego County, CA, USA (32°52'30"N, 117°15'15"W). Annual average precipitation is 22 cm, the majority of which falls between November and March. The reserve is dominated by Diegan coastal sage (Axelrod 1978), a cismontane plant community constituent of the California Floristic Province. Recent anthropogenic disturbance occurred during the early 1900s, when parts of the reserve were cleared and grazed (I. Kay, personal communication). The experimental site was located on a previously disturbed flat area in the interior of the reserve currently dominated by exotic species. Common invasive forbs in the reserve include *Erodium cicutarium*, *Hirschfeldia incana* and *Medicago polymorpha*, and common invasive annual grasses include *Avena barbata* and *Bromus diandrus* (Hickman 1993).

PLOT DESIGN AND PRE-SEASON RAINFALL TREATMENTS

To test our hypothesis that exotic annual grasses have more flexible germination cues than native species, we seeded focal species (see below) into experimental plots and imposed pulse watering events of varying magnitudes in August and September 2009. Each 2 × 2 m plot was surrounded by a 1 m buffer to minimize runoff into adjacent plots during watering. The seven watering treatments, replicated eight times, were: a 10 mm rain event in either August or September, a 20 mm rain event in either August or September, a 30 mm event in either August or September, and a control which was not watered. Pulse treatments were applied as 10 mm rainfall events per day. Each plot was watered by hand using watering cans over the course of each day, with attention given to uniform distribution of water and minimization of runoff. A total of 1920 L of water were applied during the watering process.

SEEDING OF NATIVE AND EXOTIC SPECIES

Seeds of three native focal species were collected from Scripps Coastal Reserve in December 2008 and May through July 2009 [shrubs *Artemisia californica* Less. and *Encelia californica* Nutt. and annual forb *Deinandra fasciculata* (DC.) Greene] and stored at 20 °C until planting. Prior to application seeds were sown into 10 × 10 cm monoculture subplots and lightly raked into the soil. *Artemisia californica* was

sown at a density of 1.6 g m⁻², *D. fasciculata* at 1.2 g m⁻² and *E. californica* at 6.6 g m⁻², reflecting differential germination rates in a prior seed viability analysis. Seeds of two exotic annual grasses, *Avena fatua* and *Bromus hordeaceus* (Hickman 1993), were obtained commercially (S&S Seed Co., Carpinteria, CA, USA) and 20 seeds each were sown into mesh soil-filled bags and placed under germination enclosures to assure that the seeds were not released into the reserve. Two different germination enclosure designs were used: two blocks contained enclosures consisting of a 7.5 × 16 × 2 cm copper frame and the remaining six blocks used a 10 cm diameter PVC frame with an approximate height of 5 cm. A layer of wedding veil mesh was attached over the top of each enclosure to minimize shade effects while preventing dispersal. In January 2010, germination enclosures were removed and grasses were left exposed for 48 h to assess potential herbivory by birds and small mammals, after which the contents of each enclosure (soil, mesh, grasses and remaining seeds) were removed to prevent invasion into the study area.

GERMINATION MONITORING

Germination data were collected twice per week following the start of watering treatments. The number of emerging seedlings of each species was recorded within each of the native-seeded subplots, each invasive grass enclosure, and an unseeded subplot following both August and September treatments, as well as an enclosed unseeded subplot in all plots treated in September to act as a control for potential enclosure effects. To assess seedling survival, data were collected continuously for each plot until all seedlings had succumbed to desiccation or herbivory. Occurrence of exotic grass herbivory was observational; in cases where a non-desiccated seedling could not be found inside an enclosure whose cover had clearly been punctured, cause of mortality was attributed to herbivory. Monitoring resumed in all plots after the first substantial rainfall event of the growing season (13.2 mm on 29 November 2009) and continued until March 2010 in order to evaluate the magnitude and temporal nature of native and exotic species' germination response to ambient rainfall conditions.

COMMUNITY RESPONSE AND HERBIVORY

To determine the extent to which seasonal priority effects contributed to annual community-level patterns of diversity and abundance, pre-treatment species composition and percentage areal cover were assessed in 1 m² quadrats in each plot according to a modified Daubenmire method (Daubenmire 1959) in August 2009 (when vegetation was senescent) and during peak growing season in early April 2010. Cover was also recorded of bare ground, litter, rock, mammalian disturbance (gopher mounds), and rodent droppings. Above-ground biomass was harvested from a 10 × 30 cm area in early May 2010, dried for 3 days at 40 °C and then weighed. Data on presence of rodent droppings were used as a proxy for mammalian herbivore activity. Rodent dropping cover data collected in April 2010 were used as a cumulative index of rodent activity beginning in August 2009.

SEEDBANK ANALYSIS

To assess whether experimental watering had depleted the existing seedbank, soil cores at 5 cm depth were taken from each plot in early November 2009. Samples were collected from small unseeded patches cleared of litter and immediately spread over potting soil in germination flats in the UC San Diego greenhouses and watered to maintain moist soils for 4 weeks. Germination data were collected as seedlings

emerged. Seedlings that proved difficult to identify were transplanted into pots and watered until identification was possible.

STATISTICAL ANALYSIS

We used mixed-effects models to examine how germination in the field varied by species and watering pulse in September and following winter rains, and how greenhouse germination of seedbanking exotics was influenced by the pre-season watering treatments. Species and watering pulse were categorical fixed effects; plot was treated as random accounting for the multiple species assessed in each plot. To examine specific differences between treatment levels and species we followed mixed-effects analyses with Tukey's test of all pairwise comparisons; lower-case letters shown on figures indicate significant differences ($P = 0.05$) (Bretz, Hothorn & Westfall 2010). For germination response to winter rains, we analysed all (August and September) plots together, as they shared a common unwatered control. There was extremely low germination in August resulting in a zero-dominated dataset, so we performed a chi-square test on median germination (to account for this non-normality but maintain the count nature of the data) to examine the effect of species only. Germination reflected maximum number of seedlings observed throughout the monitoring period and we square-root transformed data to meet model assumptions. A Fisher's exact test was used to assess contingency of rodent dropping presence on summer germination of exotic annual grasses. A paired t -test was performed to assess herbivory of exotic grasses after mesh covers were removed, and an unpaired t -test was used to examine differences in exotic grass germination between the two enclosure types. We used R version 2.12 (R Development Core Team 2010) for all analyses, including the package nlme for mixed effects modelling (Pinheiro *et al.* 2011).

Results

Germination following pulses of late summer irrigation varied by species, watering levels and month of pulse. In August, only exotic species germinated (one *A. fatua* individual and three *B. hordeaceus* individuals; $\chi_3^2 = 12$, $P = 0.007$) following 30 mm of water: there was no germination in response to any other water amounts or by either native species (Fig. 2a). Germination following the September pulse was higher (Fig. 2b) but with similar trends. Responses to water varied by species (water \times species: $F_{9,84} = 20.62$, $P < 0.0001$, water: $F_{3,28} = 53.15$, $P < 0.0001$), with species exhibiting very different germination rates ($F_{3,84} = 59.32$, $P < 0.0001$, Fig. 2b). Both exotic species germinated in response to the two highest pulse amounts (Fig. 2b), but *B. hordeaceus* responded more to the higher watering rate (29% and 31% of planted seeds, 20 and 30 mm, respectively) than *A. fatua* (6% and 15% of planted seeds, 20 and 30 mm, respectively). In contrast, germination of native species was nearly non-existent, with only two *E. californica* individuals germinating (in the 30 mm water addition treatment). All *A. fatua* and *B. hordeaceus* individuals that had germinated with the water addition perished in mid-October before the onset of the natural rains, but the two *E. californica* seedlings persisted until the first major autumn rain in late November. Exotic forbs *E. cicutarium* and *H. incana* germinated from the seedbank in the unseeded subplots with the highest watering treatment (mean \pm SE:

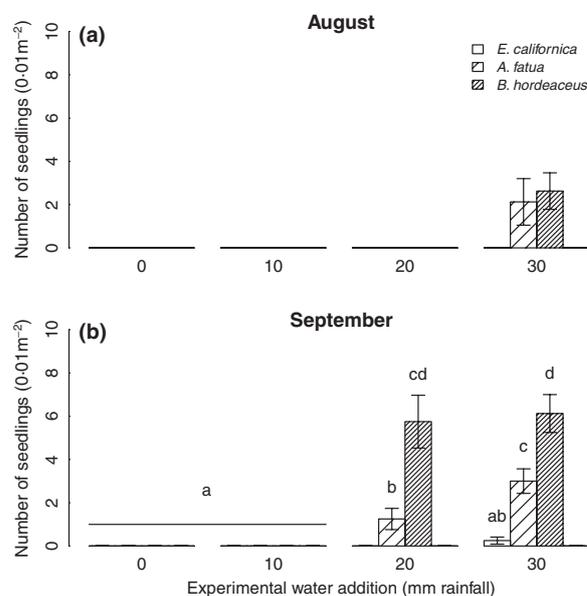


Fig. 2. Mean germination of focal native species *Encelia californica* and exotic annual grasses *Avena fatua* and *Bromus hordeaceus* (hatched) in seeded subplots following pre-season watering treatments in (a) August and (b) September. Note that native species with zero germination during this time period are not included in the figure. Bars indicate standard error ($n = 8$).

0.63 ± 0.38 and 2.00 ± 1.46 *E. cicutarium* individuals in enclosure subplots receiving 20 and 30 mm water addition, respectively; 0.13 ± 0.13 *H. incana* individuals in exposed subplots receiving 20 mm water addition). No germination of unseeded native species was observed and germination rates of unseeded exotic species did not differ between the enclosed and exposed subplots ($P = 0.12$), suggesting that seedlings were not consumed before their germination could be recorded. Germination rates of exotic annual grasses did not differ between enclosure types for August ($P = 0.76$) or September ($P = 0.65$) watering treatments.

With the onset of the winter rains exotic species (both seeded and from the seedbank) germinated more quickly than native species (Fig. 3). The effect of early-season watering on winter germination varied by species (water \times species: $F_{9,156} = 8.45$, $P < 0.0001$; water: $F_{3,52} = 16.13$, $P < 0.0001$). Germination differed strongly by species ($F_{3,156} = 97.29$, $P < 0.0001$) and was lower for exotic annual grasses in plots that had received the higher levels of summer watering (Fig. 4). The exotic annual grass *B. hordeaceus*, which was particularly likely to germinate with the watering pulse, had lower growing season germination in plots subject to large summer watering pulses (Fig. 4). Germination of *A. fatua*, which had lower germination with experimental pulses, did not have different winter germination rates among plots with different watering treatments (Fig. 4). The experimental watering did not affect germination of the seeded native shrub *E. californica* and forb *D. fasciculata*. Two additional native forbs *Camissonia bistorta* and *Crassula connata* (Hickman 1993) had significant winter germination from the seedbank which was not altered by watering treatments. Only three individual *A. californica*

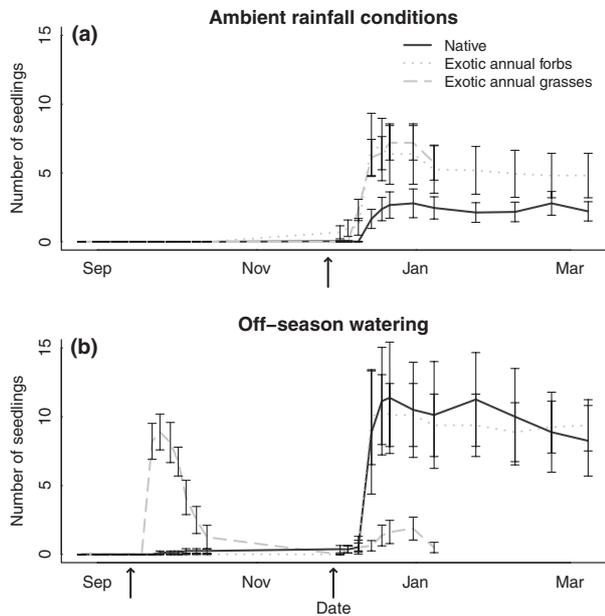


Fig. 3. (a) Mean growing season abundances of native and exotic annual grass and forb species under ambient (control) rainfall conditions. Arrow on *x*-axis denotes timing of first autumn rain. (b) Growing season abundances of native and exotic grass and forb species in plots receiving a 30 mm rainfall pulse treatment in September. Arrows on *x*-axis denote timing of off-season water application (left) and first autumn rain (right). Data are combined from seeded and uncovered unseeded subplots. Bars indicate standard error ($n = 8$).

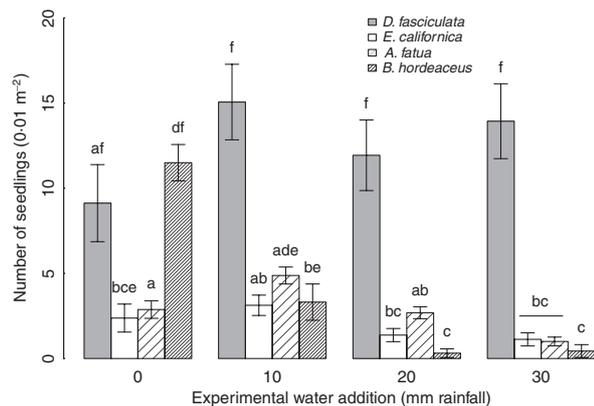


Fig. 4. Mean germination of focal native species and exotic annual grasses in seeded subplots following natural winter rains in plots watered in both August and September. Bars indicate standard error ($n = 8$ for control, $n = 16$ for each water addition level).

seedlings were observed throughout the duration of the monitoring, none of which survived. This was probably due to barriers to germination such as low seed viability or granivory. Data for *A. californica* germination were not included in our analyses or figures.

The effect of the pre-season watering pulse on greenhouse seedbank germination varied by species (water \times species: $F_{6,104} = 3.17$, $P = 0.007$; water: $F_{3,52} = 3.77$, $P = 0.016$; species: $F_{2,104} = 17.21$, $P < 0.0001$). *Erodium cicutarium* seedbank depletion was evident in 10 mm watered plots

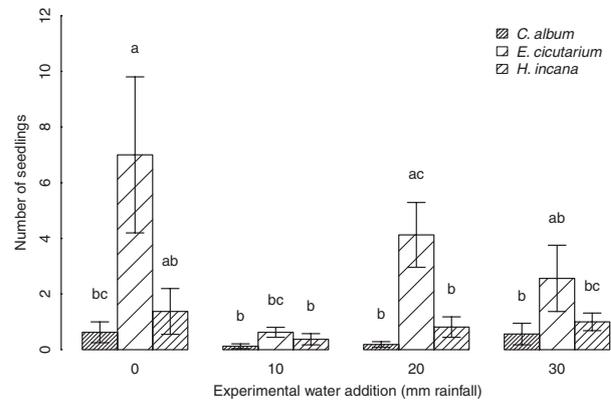


Fig. 5. Mean greenhouse germination of seedbanking exotic forbs from soil cores collected in plots after August and September water additions. Bars indicate standard error ($n = 8$ for control, $n = 16$ for each water addition level).

(Fig. 5), but this reduction was not observed for *H. incana* and *Chenopodium album*. Despite the apparent depletion of *E. cicutarium* in the seedbank of 10 mm watered plots indicated by the results of the seedbank analysis, neither percentage cover nor abundance of *E. cicutarium* was diminished by the pulse of summer irrigation in the field plots by the end of the growing season (Table S1, Supporting Information). Likewise, cover of *H. incana* and *C. album* were not influenced by the watering treatments. No native species germinated from the soil samples collected to evaluate the effects of watering pulses on the seedbank, indicative of the limited native seedbank at this site. Peak growing season total aboveground biomass was not influenced by the level of off-season water addition.

Rodent droppings were present only in plots that received 20 or 30 mm of pre-season watering treatments, where rodent droppings were observed in 38% of plots containing pulse-germinated exotic annual grass seedlings and only 9% of plots which did not contain pulse-germinated exotic annual grass seedlings ($P = 0.01$), suggesting that herbivores were attracted to the exotic grass seedlings in these plots. In early January 2010, mesh covers of each exotic annual grass germination enclosure were taken off and left open for 48 h to assess potential removal by herbivores. A substantial decrease in mean number of individuals was observed for *A. fatua* (mean \pm SE: 2.57 ± 0.26 – 1.59 ± 0.28 individuals; $t_{1,55} = 4.997$, $P < 0.0001$) as well as *B. hordeaceus* (mean \pm SE: 2.3 ± 0.57 – 1.84 ± 0.52 individuals; $t_{1,55} = 1.9651$, $P = 0.05$).

Discussion

Our results suggest that the timing of germination can play a critical role in species' success on a within-year scale by influencing which species are active at a given time. Under the scenario of ambient rainfall timing, exotic annual grasses and forbs germinated quickly with the onset of the winter rains and reached a higher abundance than native species (Fig. 3a), indicating that a seasonal priority effect may contribute to their success. Thus, our results advance research on the importance of variability in autumn precipitation to community structure

in similar assemblages (Talbot, Biswell & Hormay 1939; Pitt & Heady 1978; Bartolome 1979), by demonstrating that timing is a critical component of such variability.

EFFECTS OF SEASONAL PRIORITY EFFECTS ON COMMUNITY-LEVEL PATTERNS OF ABUNDANCE

The results of this experiment suggest that priority effects exerted via exotic germination plasticity could potentially play an important role in the successful establishment of invaders in this system. The early-active phenology of many exotic species may generally serve as an important mechanism conferring competitive superiority. Theoretical frameworks on invasion hypothesize that a fitness advantage or fundamental niche difference from resident species enables exotic species to invade and establish (MacDougall, Gilbert & Levine 2009; Wolkovich & Cleland 2011). This may apply to the invasion of exotic annual grasses, as distributional range sizes of weedy species positively correlate with germination niche breadth and higher values of performance-related traits are often linked to high fitness values conferring invasiveness (Brandle *et al.* 2003; Van Kleunen, Weber & Fischer 2010). Early germination provides exotic annual seedlings advanced access to soil resources on a temporal scale (early exposure to nutrient and water supplies) as well as on a spatial scale (greater soil area for root establishment before native species break dormancy or germinate). In addition, limitations to native seed production and dispersal augment barriers to native establishment, especially after disturbance (Seabloom *et al.* 2003a). Although focal species were seeded in separate subplots, similar germination responses are likely in mixed communities where native seedlings would benefit from reduced direct competition with exotic annual grasses.

ADVANTAGES AND DISADVANTAGES OF FLEXIBLE GERMINATION CUES

When we imposed a pre-growing season rainfall event by irrigating in late summer we found that having flexible germination cues can incur a cost. Germination of the exotic annual grasses, *A. fatua*, *B. hordeaceus*, and seedbanking exotic forbs was induced within 1 week of pre-season watering, in contrast to the negligible germination of any native species, thus supporting the hypothesis that some exotic species have more flexible germination cues than native species. Rather than conferring an advantage (Fig. 1a), however, every exotic grass individual that germinated in response to the summer watering died before the natural rains began, suggesting that these individuals suffered priority disadvantage (Fig. 1b) when cued to germinate before the true onset of the growing season.

Apparency to herbivores may have been an important component of this priority disadvantage. Plots with early-season germination had greater cover of rodent droppings, suggesting herbivory also increased in these plots. This may be due to the high pre-season demand for nutritious plant tissue and increased visual apparency in the landscape which is typically devoid of herbaceous vegetation until winter rains commence. Removal of the mesh over the exotic grass enclosures in Janu-

ary provided further evidence that herbivory may be an important control over exotic grass abundance in this system; 38% of *A. fatua* and 20% of *B. hordeaceus* individuals were removed by herbivores within a 2 day window. Browsing by native generalist herbivores may be a tenable method of biotic control during the earliest stages of invasion at sites where exotic propagule pressure is low and seedbank presence has not yet reached a threshold density overwhelming to native granivores and herbivores (Hoffmann & Moran 1998; Parker 2000). The effectiveness of native herbivore control over exotic seedling establishment may hinge on the functional response of generalist herbivores while seedlings are not yet superabundant or have not attained enough biomass to tolerate herbivory (Maron & Vila 2001).

Our findings are consistent with the hypothesis that unlike the exotic annual grasses, species native to coastal Southern California may be under selective pressure to germinate only with cool temperatures that cue the onset of the consistent winter rains (Reynolds, Corbin & D'Antonio 2001). Germination of native species took place only after the first storm that generated rain for multiple days. Data on rainfall in San Diego spanning nearly a century indicate that rains exceeding 25 mm associated with native plant germination are exceedingly rare until early December and are usually followed by equally large rains to sustain growth (Fig. S1, Supporting Information). These data provide a potential explanation for the overwhelming unresponsiveness to late summer watering in native species. Conformity of germination cues to trends in local climate variation implies that timing of germination is under selection in some systems (Kudoh *et al.* 2007). Plant communities adapted to annual cycles of prolonged drought are often comprised of long-lived drought-deciduous species whose germination is optimal late in the growing season when precipitation is reliable and soils remain moist (Harrison, Small & Mooney 1971; Williams & Hobbs 1989; Gulmon 1992; Weltzin & Tissue 2003). Coastal sage scrub species may require a greater threshold amount of rainfall coinciding with cool temperatures and shorter photoperiod in order to prompt phenological events such as germination or seasonal increase in photosynthetic capacity (Comstock & Ehleringer 1986; Padgett, Kee & Allen 2000). In semi-arid plant communities where interannual climate variation is common, seed dormancy may buffer populations against loss of individuals germinating under inopportune conditions (Keeley 1991; Pake & Venable 1996; Facelli, Chesson & Barnes 2005). Combinations of specific environmental cues are likely to serve as indicators of reliable winter rains to support late-season growth and establishment for plant species native to semi-arid Mediterranean-type ecosystems (Levine, McEachern & Cowan 2008).

The response of exotic annual forbs to summer watering was not as strong as the responses of the exotic annual grasses. Apart from *E. cicutarium*, germination of exotic forbs was low and not influenced by watering treatments. Results from the seedbank study indicated a significant post-treatment reduction of the *E. cicutarium* seedbank following the lowest level of watering, suggesting that in some cases, summer watering had led to substantial seedbank depletion. Despite the implications

of the seedbank study, evidence for post-treatment seedbank depletion of *E. cicutarium* was not displayed at the community level over the course of the growing season. *Erodium cicutarium* remained the dominant species across all experimental plots in both coverage and number of individuals. The fact that the experimental pulse of summer watering was ineffectual at limiting growing-season abundance of *E. cicutarium* is likely to be a reflection of a high-density seedbank at this site or lack of amenable temperature germination cues (Rice 1985).

RESTORATION IMPLICATIONS IN ECOSYSTEMS WITH SEASONAL RAINFALL

Germination plasticity of exotic grasses may contribute to their invasion success in semi-arid and Mediterranean-type ecosystems if they are able to germinate quickly with the onset of seasonal rains. Our results indicate that aspects of germination plasticity can also be manipulated, however, by exploiting exotic species' flexible germination cues. Pre-growing season irrigation pulses may serve as a viable restoration technique in many systems undergoing early stages of exotic grass invasion, given several following caveats. (i) Species-level variation in the flexibility of germination cues may help to determine the context in which pre-season watering pulses would be effective at reducing invader abundance. The results of this experiment suggest that this method could potentially be well-suited to sites and systems in which annual grasses are the dominant invader, but not necessarily annual forbs. Further research efforts should test the generality of these results across a greater number of species and functional groups, including those found in semi-arid systems other than California. (ii) Care should be taken to ensure that the watering pulse is applied adequately in advance of natural rains. Long-term trends in local climate data should indicate that large rainfall events are not likely to occur early in the growing season, because exotic grasses that germinate with off-season watering should not receive any growth-sustaining water before they succumb to desiccation/herbivory, and if native species germinate following rains too soon after the off-season watering, they may be suppressed by exotic seedlings that germinated with the off-season watering. (iii) Restoration sites should be chosen that contain sufficient generalist herbivore populations to constrain survival of exotic grass seedlings. In order to maximize apparency to herbivores, areas should be chosen in which palatable vegetation is typically absent in the pre-season. (iv) Implications for management become increasingly robust from multi-year experimental data collection. Off-season watering pulses should be applied over several consecutive years in order to reduce each successive generation of exotic annuals' contribution to the following year's seedbank. Otherwise, competitive release of native species may only occur for 1 year at sites where the exotic seedbank is well-established.

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References

- Abraham, J.K., Corbin, J.D. & D'Antonio, C.M. (2009) California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. *Plant Ecology*, **201**, 445.
- Axelrod, D.I. (1978) The origin of coastal sage vegetation, Alta and Baja California. *American Journal of Botany*, **65**, 1117–1131.
- Baker, H.G. (1989) Sources of the naturalized grasses and herbs in California. *Grassland Structure and Function* (eds L.F. Huenneke & H.A. Mooney), pp. 29–36. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Barbour, M., Pavlik, B.M., Drysdale, F. & Lindstrom, S. (1991) California vegetation: diversity and change. *Fremontia*, **19**, 3.
- Bartolome, J.W. (1979) Germination and seedling establishment in California annual grassland. *Journal of Ecology*, **67**, 273–281.
- Belyea, L.R. & Lancaster, J. (1999) Assembly rules within a contingent ecology. *Oikos*, **86**, 402–416.
- Booth, M.S., Caldwell, M.M. & Stark, J.M. (2003) Overlapping resource use in three great basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology*, **91**, 36–48.
- Brandle, M. *et al.* (2003) Distributional range size of weedy plant species is correlated to germination patterns. *Ecology*, **84**, 136–144.
- Bretz, F., Hothorn, T. & Westfall, P. (2010) *Multiple Comparisons Using R*. CRC Press, Boca Raton, FL.
- Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, **2**, 436–443.
- Carlsen, T.M., Menke, J.W. & Pavlik, B.M. (2000) Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. *Restoration Ecology*, **8**, 18.
- Colautti, R.I., Grigorovich, I. & MacIsaac, H. (2006) Propagule pressure: a null model for biological invasions. *Biological Invasions*, **8**, 1023–1037.
- Coleman, H.M. & Levine, J.M. (2007) Mechanisms underlying the impacts of exotic annual grasses in a coastal California meadow. *Biological Invasions*, **9**, 65.
- Comstock, J. & Ehleringer, J.R. (1986) Photoperiod and photosynthetic capacity in *Lotus scoparius*. *Plant, Cell and Environment*, **9**, 609.
- Corbin, J.D. & D'Antonio, C.M. (2004) Competition between native perennial and exotic annual grasses: implications for an historical invasion. *Ecology*, **85**, 1273–1283.
- Crampton, B. (1974) *Grasses in California*. University of California Press, Berkeley and Los Angeles, CA.
- D'Antonio, C.M., Hughes, R.F. & Vitousek, P.M. (2001) Factors influencing dynamics of two invasive C4 grasses in seasonally dry Hawaiian woodlands. *Ecology*, **82**, 89–104.
- D'Antonio, C.M., Malmstrom, C., Reynolds, S.A. & Gerlach, J. (2007) Ecology of invasive non-native species in California grassland. *California Grasslands: Ecology and Management* (eds M.R. Stromberg, J.D. Corbin & C.M. D'Antonio), pp. 67–83. University of California Press, California.
- Daubenmire, R. (1959) A canopy-coverage method of vegetation analysis. *Northwest Science*, **33**, 43.
- Davidson, A.M., Jennions, M. & Nicotra, A.B. (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters*, **14**, 419–431.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.
- Deering, R.H. & Young, T.P. (2006) Germination speeds of exotic annual and native perennial grasses in California and the potential benefits of seed priming for grassland restoration. *Grasslands*, **16**, 14–15.
- DeFalco, L., Fernandez, G. & Nowak, R. (2007) Variation in the establishment of a non-native annual grass influences competitive interactions with Mojave Desert perennials. *Biological Invasions*, **9**, 293–307.
- Eliason, S.A. & Allen, E.B. (1997) Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology*, **5**, 245.
- Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.

- Espigares, T. & Peco, B. (1993) Mediterranean pasture dynamics: the role of germination. *Journal of Vegetation Science*, **4**, 189–194.
- Facelli, J.M., Chesson, P. & Barnes, N. (2005) Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. *Ecology*, **86**, 2998–3006.
- Godoy, O. *et al.* (2009) Flowering phenology of invasive alien plant species compared with native species in three Mediterranean-type ecosystems. *Annals of Botany*, **103**, 485–494.
- Grime, J.P. *et al.* (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology*, **69**, 1017–1059.
- Grman, E. & Suding, K.N. (2010) Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. *Restoration Ecology*, **18**, 664–670.
- Gulmon, S.L. (1992) Patterns of seed germination in Californian serpentine grassland species. *Oecologia*, **89**, 27–31.
- Harrison, A.T., Small, E. & Mooney, H.A. (1971) Drought relationships and distribution of two Mediterranean-climate California plant communities. *Ecology*, **52**, 869–875.
- Hawkes, C.V. *et al.* (2006) Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. *Plant and Soil*, **281**, 369.
- Heady, H.F. (1958) Vegetational changes in the California annual type. *Ecology*, **39**, 402–416.
- Hickman, J.C. (1993) *The Jepson Manual: Higher Plants of California*. University of California Press, Berkeley and Los Angeles, California.
- Hierro, J.L. *et al.* (2009) Germination responses of an invasive species in native and non-native ranges. *Oikos*, **118**, 529–538.
- Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, **6**, 324–337.
- Hobbs, R.J. & Mooney, H.A. (1985) Community and population dynamics of serpentine grassland annuals in relation to Gopher disturbance. *Oecologia*, **67**, 342–351.
- Hoffmann, J.H. & Moran, V.C. (1998) The population dynamics of an introduced tree, *Sesbania punicea*, in South Africa, in response to long-term damage caused by different combinations of three species of biological control agents. *Oecologia*, **114**, 343–348.
- Keeley, J.E. (1991) Seed germination and life history syndromes in the California chaparral. *Botanical Review*, **57**, 81–116.
- Kudoh, H. *et al.* (2007) Does invasion involve alternation of germination requirements? A comparative study between native and introduced strains of an annual Brassicaceae, *Cardamine hirsuta*. *Ecological Research*, **22**, 869.
- Lambrinos, J.G. (2006) Spatially variable propagule pressure and herbivory influence invasion of chaparral shrubland by an exotic grass. *Oecologia*, **147**, 327.
- Levine, J.M., McEachern, K.A. & Cowan, C. (2008) Rainfall effects on rare annual plants. *Journal of Ecology*, **96**, 795.
- Liu, H. & Stiling, P. (2006) Testing the enemy release hypothesis: a review and meta-analysis. *Biological Invasions*, **8**, 1535–1545.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- Lulow, M.E. (2006) Invasion by non-native annual grasses: the importance of species biomass, composition, and time among California native grasses of the central valley. *Restoration Ecology*, **14**, 616–626.
- MacDougall, A.S., Gilbert, B. & Levine, J.M. (2009) Plant invasions and the niche. *Journal of Ecology*, **97**, 609.
- Mack, R.N. *et al.* (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.
- Maron, J.L. & Vila, M. (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, **95**, 361–373.
- Marushia, R.G., Cadotte, M.W. & Holt, J.S. (2010) Phenology as a basis for management of exotic annual plants in desert invasions. *Journal of Applied Ecology*, **47**, 1290–1299.
- Minnich, R.A. (2008) *California's Fading Wildflowers: Lost Legacy and Biological Invasions*. University of California Press, Berkeley and Los Angeles, CA.
- Padgett, P.E., Kee, S.N. & Allen, E.B. (2000) The effects of irrigation on revegetation of semi-arid coastal sage scrub in southern California. *Environmental management*, **26**, 427.
- Pake, C.E. & Venable, D.L. (1996) Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, **77**, 1427–1435.
- Parker, I.M. (2000) Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecological Applications*, **10**, 726–743.
- Pimentel, D., Zuniga, R. & Morrison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273–288.
- Pinheiro, J., Bates, J.D., DebRoy, S., Sarkar, D. & R Development Core Team (2011) *nlme: Linear and Nonlinear Mixed Effects Models. R Package Version 3.1–102*.
- Pitt, M.D. & Heady, H.F. (1978) Responses of annual vegetation to temperature and rainfall patterns in northern California. *Ecology*, **59**, 336–350.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. Vienna, Austria. <http://www.R-project.org>.
- Reynolds, S.A., Corbin, J.D. & D'Antonio, C.M. (2001) The effects of litter and temperature on the germination of native and exotic grasses in a coastal California grassland. *Madrone*, **48**, 230–235.
- Rice, K.J. (1985) Responses of *Erodium* to varying microsites: the role of germination cueing. *Ecology*, **66**, 1651–1657.
- Richards, C.L. *et al.* (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*, **9**, 981–993.
- Sax, D.F. *et al.* (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution*, **22**, 465–471.
- Seabloom, E.W. *et al.* (2003a) Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecological Applications*, **13**, 575–592.
- Seabloom, E.W. *et al.* (2003b) Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 13384.
- Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution*, **17**, 170–176.
- Talbot, M.W., Biswell, H.H. & Hormay, A.L. (1939) Fluctuations in the annual vegetation of California. *Ecology*, **20**, 394–402.
- Tevis Jr, L. (1958) Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology*, **39**, 681–688.
- Van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, **13**, 235.
- Weltzin, J.F. & Tissue, D.T. (2003) Resource pulses in arid environments: patterns of rain, patterns of life. *New Phytologist*, **157**, 171–173.
- Went, F.W. (1949) Ecology of desert plants. II: The effect of rain and temperature on germination and growth. *Ecology*, **30**, 1–13.
- Williams, K. & Hobbs, R.J. (1989) Control of shrub establishment by spring-time soil water availability in an annual grassland. *Oecologia*, **81**, 62–66.
- Wolkovich, E.M. & Cleland, E.E. (2011) The phenology of plant invasions: a community ecology perspective. *Frontiers in Ecology and the Environment*, **9**, 287–294.
- Young, T.P., Chase, J.M. & Huddleston, R.T. (2001) Community succession and assembly. *Ecological Restoration*, **19**, 5.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Timing of first 1 cm and 2.5 cm rains in San Diego based on records from 1914 to 2007.

Table S1. Percentage cover of native and exotic seedbanking species measured in 1 m² quadrats during peak growing season 2010.

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